APPENDIX G

EXPLORATION OF RECRUITS PER SPAWNER ANALYSIS

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Overview

All models are wrong, some are useful.
—Box 1976

A generic approach for identifying a viable productivity-abundance criterion involves estimating extinction risk using a population dynamics model and determining the threshold where productivity and abundance parameters just yield an acceptable risk. The results of this sort of analysis can be plotted in a "viability curve," where every point on the curve represents a productivity-abundance combination with identical extinction risk (Figure G.1). A key issue in developing a specific method from this generic approach is defining the form of the population dynamics model used to estimate extinction risk. In Table G.1, we describe a number of relatively simple population dynamics models that have been applied to salmon and could potentially be used to estimate extinction risk. Many of these models are discussed in Hilborn and Walters (1992).

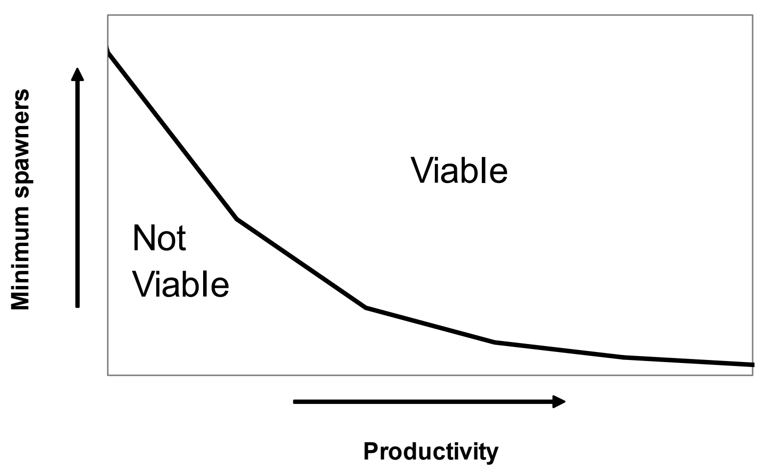

Figure G.1 Conceptual graph of the relationship between productivity, population size, and extinction risk. The curve in the figure represents combinations of size and productivity that just exactly have the acceptable extinction risk.

All of these models except the "constant recruitment" model involve projecting the number of recruits as a stochastic function of the number of spawners. The constant recruitment model assumes that recruitment fluctuates stochastically around some fixed value, regardless of the number of spawners. In addition to a parameter describing the variation in the spawner-recruit relationship, some of the models include additional terms, such as carrying capacity or marine survival. It is important to emphasize that recruitment curves describe an average relationship between recruits and spawners from which individual years will surely deviate, and to reiterate the point made in the opening quote of this appendix, none of the models in Table G.1 describes the true relationship between recruits and spawners. The challenge is determining whether any of them may be useful for setting viability criteria. We return to this point in the section below on model selection.

Table G.1 Population dynamics models proposed for salmon populations.

Model Number	**Model Name**	**Equation**[a]
Model 0	Random walk	$R = S\exp(\sigma_0 Z)$
Model 1	Random walk with drift; stochastic exponential growth or decline	$R = S\exp(a_1 + \sigma_1 Z)$
Model 2	Constant recruitment	$R = b_2\exp(\sigma_2 Z)$
Model 3	Stochastic hockey stick; stochastic exponential growth with a ceiling	$R = \min(S, b_3)\exp(a_3 + \sigma_3 Z)$
Model 4	Ricker; stochastic logistic	$R = S\exp(a_4 + b_4 S + \sigma_4 Z)$
Model 5	Beverton-Holt	$R = \dfrac{a_5 S}{1 + \dfrac{a_5}{b_5} S}\exp(\sigma_5 Z)$
Model 6	Ricker juvenile production with given marine survival	$R = c_6 S\exp(a_6 + b_6 S + \sigma_6 Z)$

[a] In the equations,

S_t = the number of spawners
R = the number of recruits
Z = a unit normal random variable
$\sigma_\#$ = the standard deviation of the process error
$a_\#$ and $b_\#$ = equation-specific parameters, with the $a_\#$ parameter relating in some way to "intrinsic productivity" and the $b_\#$ parameter relating in some way to "capacity"
c_6 = a marine survival parameter; the a_6 and b_6 parameters in this equation relate to the production of juvenile outmigrants from spawners

Viability Curves

In Figures G.2 to G.5, we present several viability curves associated with the recruitment functions in Table G.1. The extinction risk associated with any particular parameter combination for a given model is found by simulating a large number of population trajectories and counting the fraction of trajectories that drop below the quasi-extinction risk threshold within the given time horizon. The intrinsic productivity axis in the curves refers to the number of recruits per spawner at very low (approaching 0) abundance. Exactly how the intrinsic productivity value relates to extinction risk depends on the specific form of the population dynamics model. In all the models, the intrinsic productivity provides an indication of population resilience, which is the tendency of the population to return toward an equilibrium value if perturbed to low abundance. The abundance axis in the curves refers to the point estimate equilibrium abundance. The initial population size for the population trajectories was the equilibrium (or mean equilibrium) abundance value for the Beverton-Holt and Ricker curves, and the carrying capacity for the hockey-stick curve. The shape of the viability curve was found by a grid search of the parameter space to identify productivity-abundance combinations with equivalent risk. This meant varying

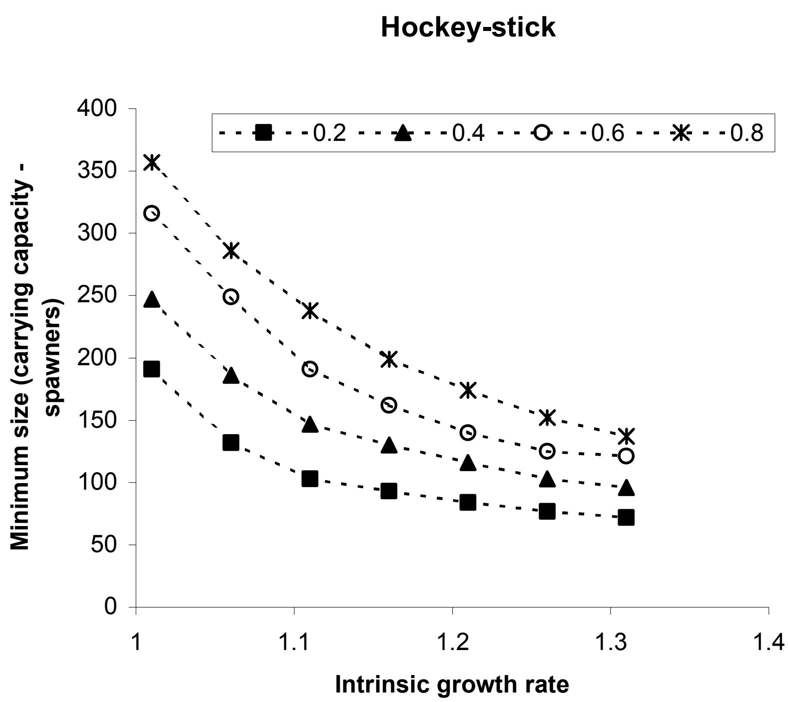

Figure G.2 Viability curves based on hockey-stick recruitment function. The different curves are for different levels of environmental variability. The viability curves were generated for a semelparous population where the average percentages of individuals spawning at a given age are: age 1 = 0%, age 2 = 1%, age 3 = 19%, age 4 = 57%, and age 5 = 23%. This life-history structure is typical of that observed for chinook salmon. In this model, the equilibrium abundance is the carrying capacity. Every point on a curve has the same extinction probability. In this example, the extinction probability is a 5% probability of declining to a four-year average of 50 spawners in 100 years.

the productivity, capacity, and process error variance parameters (i.e., the *a*, *b* and σ^2 parameters in Table G.1) and fixing all other parameters. In addition to the equilibrium abundance, the figures show the viability curves in terms of the "carrying capacity." The carrying capacity has different biological interpretations for the different models, so they are not directly comparable. However, the shape of these capacity curves is informative.

A common feature of all the viability curves we have examined is that as the intrinsic productivity parameter exceeds about 1.1, the number of spawners needed for a viable population (i.e., a population that has a risk of less than 5% of declining to a four-year average of 50 fish in 100 years) declines to a few hundred fish. For the example, Ricker and Beverton-Holt curves in Figures G.3 and G.4, the viable equilibrium abundance is less than 200 spawners and relatively constant as long as the intrinsic productivity parameter is above 1. The parameter that varies more substantially in these models is the carrying capacity parameter, although it is a parameter we can never directly observe. If a population can be demonstrated to have an intrinsic productivity substantially above 1, the actual abundance of the population becomes much less relevant. A resilient population will likely be viable, even if it is very small.

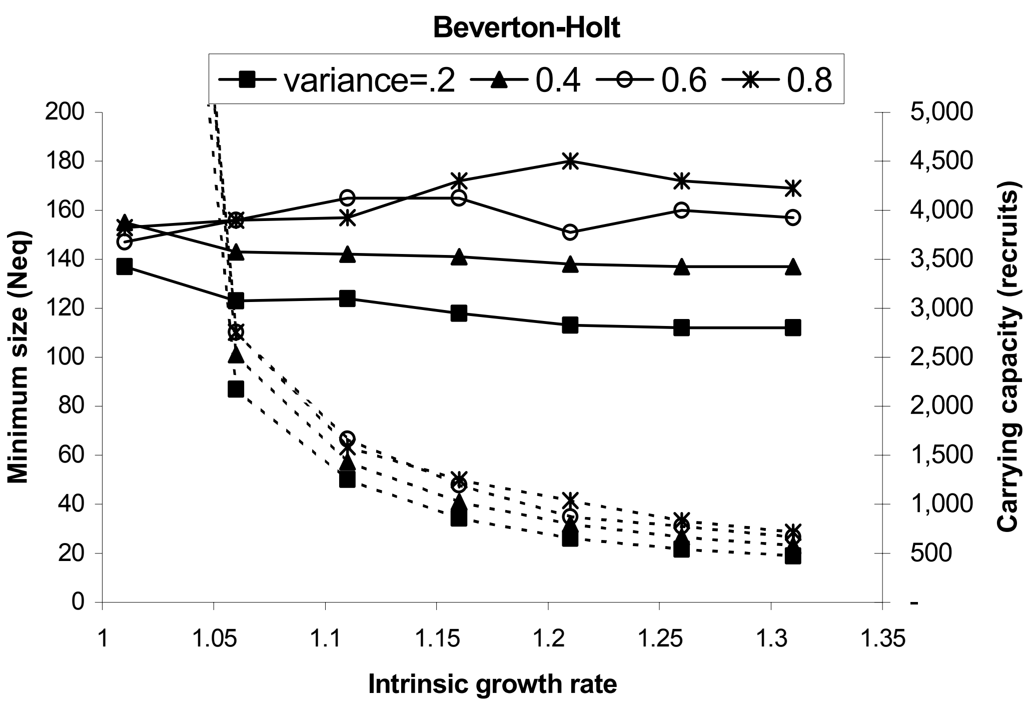

Figure G.3 Viability curves based on Beverton-Holt recruitment function. The different curves are for different levels of environmental variability. The viability curves were generated for a semelparous population where the average percentages of individuals spawning at a given age are: age 1 = 0%, age 2 = 1%, age 3 = 19%, age 4 = 57%, and age 5 = 23%. This life-history structure is typical of that observed for chinook salmon. The solid lines show equilibrium abundance and the dashed lines show the value of the "capacity" parameter in the Beverton-Holt function. Every point on a curve has the same extinction probability. In this example, the extinction probability is a 5% probability of declining to a four-year average of 50 spawners in 100 years.

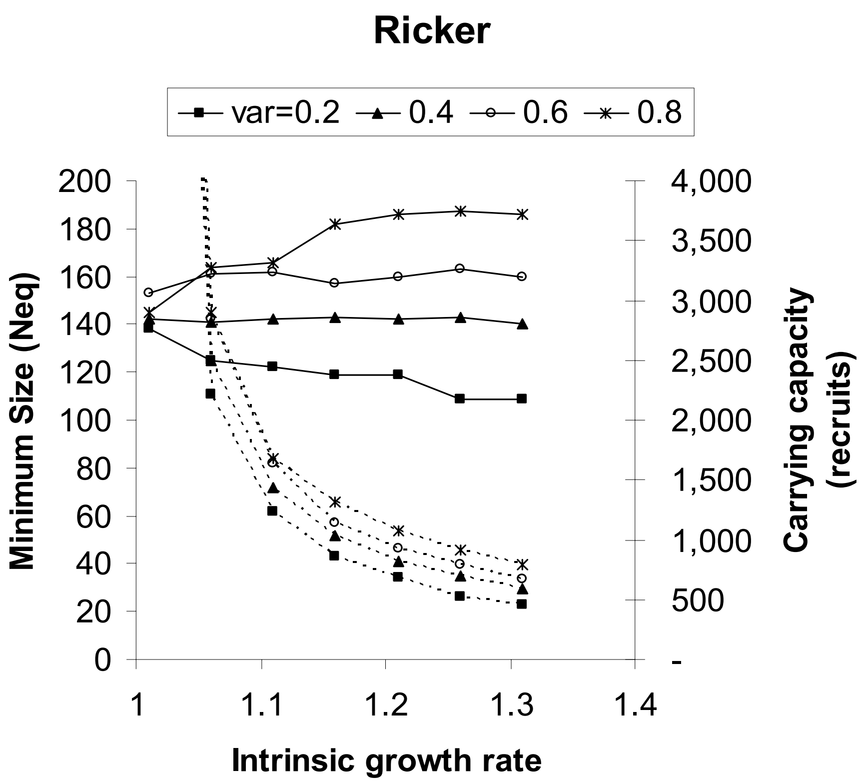

Figure G.4 Viability curves based on Ricker recruitment function. The different curves are for different levels of environmental variability. The viability curves were generated for a semelparous population where the average percentages of individuals spawning at a given age are: age 1 = 0%, age 2 = 1%, age 3 = 19%, age 4 = 57%, and age 5 = 23%. This life-history structure is typical of that observed for chinook salmon. The solid lines show equilibrium abundance, and the dashed lines show the value of the "capacity" parameter in the Ricker function. Every point on a curve has the same extinction probability. In this example, the extinction probability is a 5% probability of declining to a four-year average of 50 spawners in 100 years.

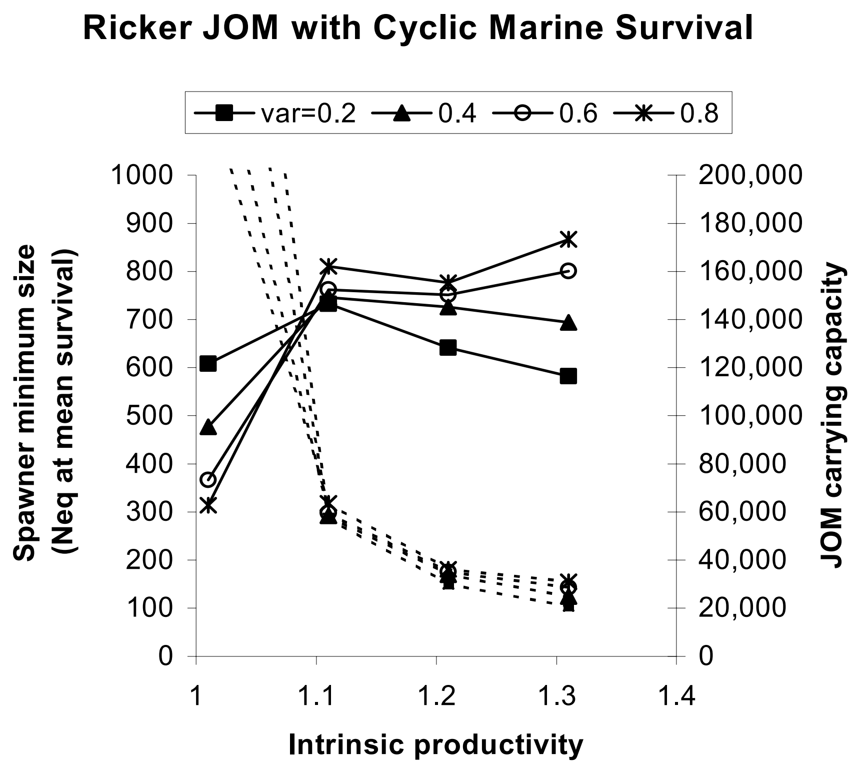

Figure G.5 Viability curves based on Ricker recruitment function for juvenile outmigrants with a cycle in marine survival. The different curves are for different levels of environmental variability. The viability curves were generated for a semelparous population where the average percentages of individuals spawning at a given age are: age 1 = 0%, age 2 = 1%, age 3 = 19%, age 4 = 57%, and age 5 = 23%. This life-history structure is typical of that observed for chinook salmon. The intrinsic productivity refers to the production of juvenile outmigrants. The ocean cycle in survival was a sine wave of 40 years' length with a mean survival of 0.05 and an amplitude of 0.03, beginning in year 0 of the cycle. The solid lines show equilibrium abundance of spawners, and the dashed lines show the value of the "capacity" parameter in the Ricker function for juveniles. Every point on a curve has the same extinction probability. In this example, the extinction probability is a 5% probability of declining to a four-year average of 50 spawners in 100 years.

Estimating Intrinsic Productivity

A key to evaluating a population's viability of using this approach is to estimate the intrinsic productivity. One of the great challenges with this general approach is determining which model, if any, might be appropriate for estimating intrinsic productivity. We can potentially look to existing abundance time series to determine which of the potential models is the "best approximating model" for this purpose (Burnham and Anderson 1998). Figure G.6 is an example of a spawner abundance time series. With information about the age structure of the population (and in some cases, numbers of hatchery spawners), it is possible to estimate how many recruits were naturally produced from each year's spawning (Figure G.7). To determine which of the proposed model forms may be useful as approximating models for setting criteria, parameters for each model were estimated from available time series and the models were statistically compared (e.g., Figure G.8). Formal model selection analysis has been relatively rare in fisheries management, and models are often adopted without adequate consideration of the alternatives.

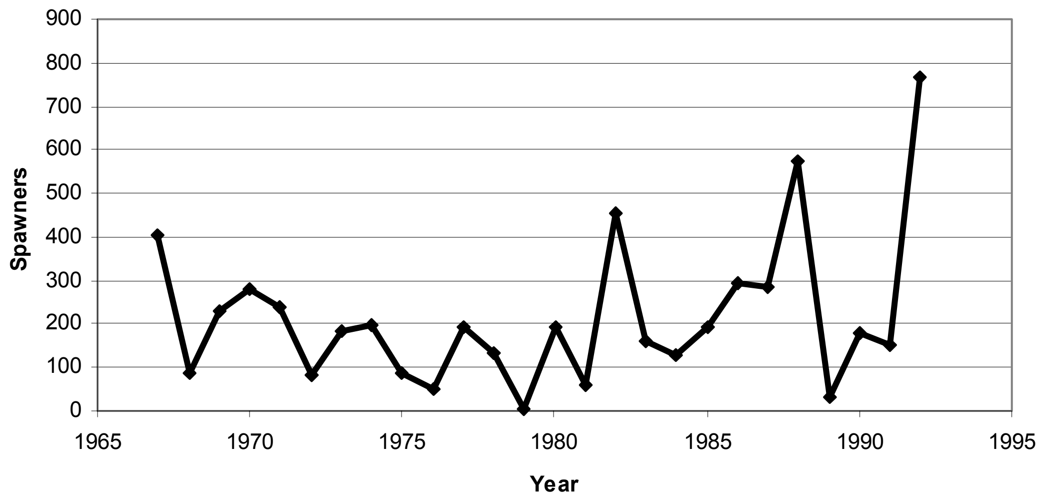

Figure G.6 Lower Columbia Gorge tributary chum salmon spawner abundance.

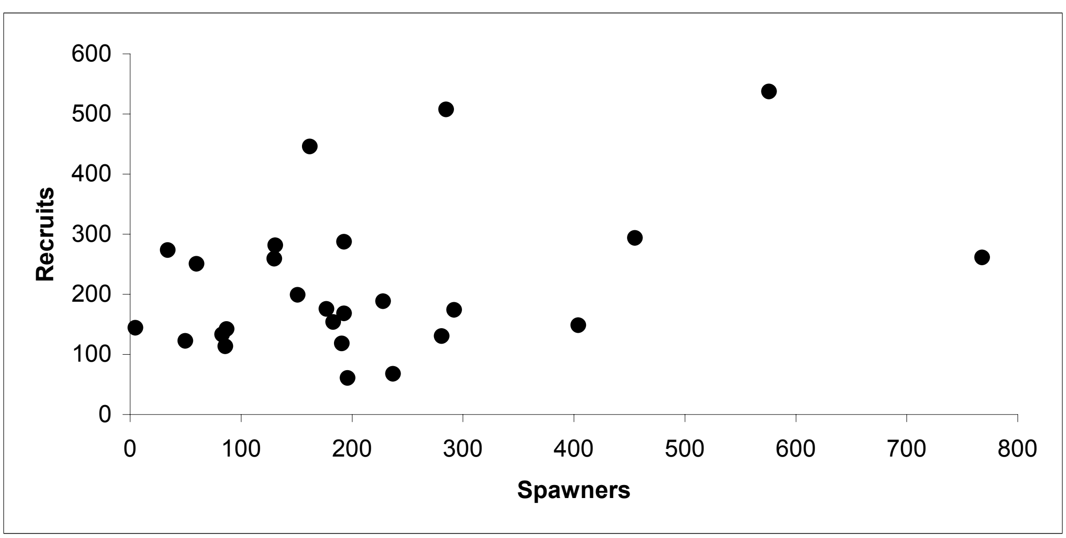

Figure G.7 Lower Columbia Gorge tributary chum salmon recruits versus spawners.

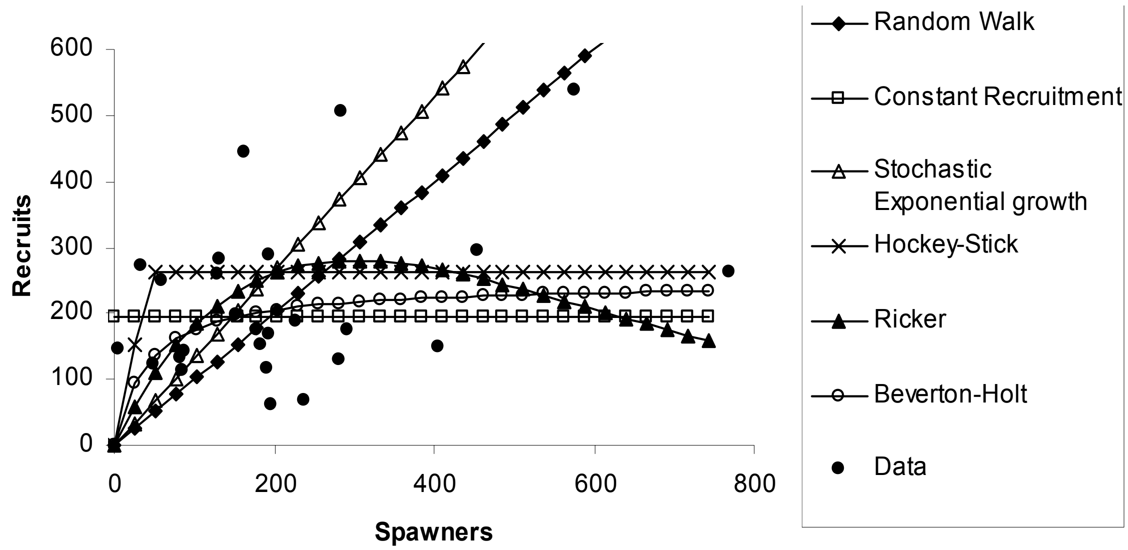

Figure G.8 Recruitment curves for lower Columbia Gorge tributary chum salmon.

Comparing Models

A number of different approaches exist for evaluating the relative utility of nonnested models. Among these approaches, the Aikake Information Criterion (AIC) method (Akaike 1973) addresses the question that is most relevant; i.e., how much do each of the models differ from the “true” process (Burnham and Anderson 1998). The AIC is a standard statistical measure of how well a model fits a data set, given a parameter set and assumptions about the error distribution. It is useful because it penalizes models in proportion to the number of parameters they have, without which we would not be able to compare larger models with smaller models. We used a version of the AIC that is corrected for small sample sizes: $AIC_c = 2(-\ln(L)) + (2p + 2*p*(p+1))/(n-p-1)$ (Burnham and Anderson 1998).

Other methods that can be used to select among models include likelihood ratio tests and comparing R^2 values associated with each model. In addition, several tests have been developed specifically to detect density dependence in abundance time series (e.g., Dennis and Taper 1994, Bulmer 1975, Pollard et al. 1987, Ruesink 2000, Shenk et al. 1998). All these methods are conceptually different from the AIC approach and have fundamental theoretical limitations. In our analysis, we have concentrated on the AIC evaluation.

We have estimated parameters for all available WLC spawner data sets for models 0–5 in Table G.1, then calculated AICc difference values to identify the best approximating models. The results are in Table G.2a-g. There are no fixed thresholds for interpreting the AIC difference values, but there are some general rules of thumb (Burnham and Anderson 1998). The AICc difference value for the best model is 0. If the AIC difference between the best model and the model with the lowest AIC is less than 2, then the second model provides a very good approximation relative to the best model, and the models might be given equal consideration. If the AIC difference value is greater than 10, the model is not a very good approximating model relative to the best model and is not very well supported by the data. If the AIC difference is between 2 and 10, the interpretation is less clear, and the biology of the situation and the question being asked should drive how the model is considered.

For 20 of 32 populations examined, the best approximating model identified using the AIC method was the constant recruitment model (Figure G.9). The Ricker model was identified as the best approximating model for six populations, but for four of them the AIC difference value for the constant recruitment model was less than 2, and either the Beverton-Holt or the hockey-stick models were also within 2, so the models are approximately equally good. For 12 of the 32 populations, at least one of the density-dependent recruitment models (i.e., hockey-stick, Ricker, or Beverton-Holt) had a low AIC difference value and could be considered a contender as the best approximating model (Figure G.10). The constant recruitment model is interesting because it is the only model examined that assumes there is no relationship between the number of spawners and the number of recruits; the number of recruits is assumed to fluctuate around a constant value. The constant recruitment model is biologically implausible if extrapolated to very low spawner numbers because at the extreme, zero spawners must yield zero recruits. However, the fact that this model was selected as the best approximating model suggests that there is little data in the range of very low abundance to exclusively support one of the models that explicitly includes a relationship between spawners and recruits. Because there are few data at low abundance, there is very little information from which to estimate the intrinsic productivity. This is also reflected in the large confidence intervals on the intrinsic productivity estimates of individual models. The ability to estimate intrinsic productivity as evaluated by the model selection analysis does not seem to improve with increased length of the time series (Figures G.11 and G.12).

Table G.2.a Lower Columbia River late-fall (bright) chinook salmon population parameter estimates and model comparison. Except as noted, recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.) Exceptions to these spawner and recruit definitions occur because of data limitations.

Population	Model[a]	a	b	σ^2	AICc	Relative AICc
Lewis River	Random walk			0.86 (0.61-1.11)	37.50	10.82
	Constant recruitment		19,769 (15,086-24,451)	0.48 (0.23-0.73)	27.24	0.56
	Random walk with trend	1.5 (1.08-2.1)		0.73 (0.35-0.98)	36.13	9.44
	Hockey-stick	2.4 (1.8-3.6)	19,769 (15,086-26,012)	0.48 (0.23-0.73)	30.41	3.73
	Ricker	**6.9 (3.3-15)**	**22,890 (19,769-33,816)**	**0.48 (0.23-0.61)**	**26.69**	**0.00**
	Beverton-Holt	25 (5.1-25)	21,329 (16,647-32,255)	0.48 (0.23-0.73)	30.99	4.30
Sandy River[b]	**Random walk**			**0.73 (0.48-0.86)**	**17.21**	**0.00**
	Constant recruitment		753 (506-1,247)	0.73 (0.35-0.98)	22.62	5.40
	Random walk with trend	0.94 (0.6-1.4)		0.73 (0.35-0.73)	21.37	4.15
	Hockey-stick	1.15 (0.6-2.7)	918 (588-1,494)	0.61 (0.35-0.73)	28.11	10.90
	Ricker	1.08 (0.65-12)	2,564 (671-2,564)	0.73 (0.23-0.73)	28.34	11.13
	Beverton-Holt	1.4 (0.75-25)	2,564 (835-2,564)	0.73 (0.35-0.86)	28.41	11.20

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference <2 are highlighted in light gray.

[b] Recruits based on natural-origin escapement, not preharvest.

Table G.2.b Lower Columbia River spring chinook salmon population parameter estimates and model comparison. Except as noted, recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.) Exceptions to these spawner and recruit definitions occur because of data limitations.

Population	Model[a]	a	b	σ^2	AICc	Relative AICc
Cowlitz River[b]	Random walk			0.73 (0.61-0.86)	35.68	23.23
	Constant recruitment		**315 (262-351)**	**0.35 (0.23-0.35)**	**12.45**	**0.00**
	Random walk with trend	1.15 (0.85-1.5)		0.73 (0.48-0.86)	37.95	25.50
	Hockey-stick	3.3 (2.1-3.6)	315 (262-351)	0.35 (0.23-0.35)	15.62	3.17
	Ricker	2.1 (1.5-3.9)	422 (333-511)	0.48 (0.35-0.48)	26.60	14.15
	Beverton-Holt	25 (4.5-25)	333 (280-422)	0.35 (0.23-0.35)	15.79	3.34

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference <2 are highlighted in light gray.

[b] Recruits based on natural-origin escapement, not preharvest.

Table G.2.c Lower Columbia River fall chinook salmon population parameter estimates and model comparison. Except as noted, recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural -origin spawners). Exceptions to these spawner and recruit definitions occur because of data limitations.

Population	Model[a]	a	b	σ^2	AICc	Relative AICc
Big White Salmon	Random walk			1.62 (1.24-1.87)	58.53	20.18
	Constant recruitment		**901 (732-1,238)**	**0.73 (0.48-0.86)**	**38.35**	**0.00**
	Random walk with trend	3 (1.8-5.1)		1.11 (0.86-1.24)	50.42	12.07
	Hockey-stick	6.9 (3.6-9.9)	1,069 (732-1,743)	0.73 (0.48-0.86)	40.39	2.04
	Ricker	6.9 (4.5-11)	1,575 (1,069-2,248)	0.73 (0.48-0.86)	41.00	2.66
	Beverton-Holt	19 (6.6-25)	1,238 (901-2,080)	0.73 (0.48-0.86)	40.54	2.19
Coweeman River	Random walk			2.12 (1.74-2.37)	62.37	31.30
	Constant recruitment		**994 (734-1,254)**	**0.61 (0.48-0.73)**	**31.07**	**0.00**
	Random walk with trend	6 (3.6-9.3)		1.11 (0.48-1.36)	46.21	15.14
	Hockey-stick	11 (7.8-25)	1,254 (864-1,774)	0.61 (0.35-0.61)	32.97	1.90
	Ricker	13 (9.6-20)	1,644 (1,254-2,294)	0.61 (0.35-0.61)	31.15	0.08
	Beverton-Holt	25 (13-25)	1,384 (994-2,684)	0.61 (0.35-0.73)	32.76	1.69
Cowlitz River	Random walk			1.24 (0.48-1.74)	44.25	12.16
	Constant recruitment		1,377 (872-2,051)	0.86 (0.48-0.98)	36.87	4.78
	Random walk with trend	0.6 (0.6-0.96)		1.11 (0.48-1.49)	44.74	12.65
	Hockey-stick	1 (0.75-1.8)	1,545 (1,040-2,388)	0.86 (0.35-0.98)	39.72	7.64
	Ricker	**3.9 (1.5-8.4)**	**2,051 (1,545-3,566)**	**0.61 (0.23-0.73)**	**32.08**	**0.00**
	Beverton-Holt	25 (1.8-25)	1,545 (1,040-3,735)	0.86 (0.35-0.98)	40.42	8.33

Table G.2.c cont.

East Fork Lewis River	Random walk			0.86 (0.61-1.11)	37.28	14.33
	Constant recruitment		**573 (460-686)**	**0.48 (0.35-0.61)**	**22.95**	**0.00**
	Random walk with trend	1.8 (1.4-2.4)		0.61 (0.35-0.73)	30.96	8.01
	Hockey-stick	3 (1.8-3.9)	573 (460-686)	0.48 (0.23-0.48)	25.10	2.15
	Ricker	5.1 (2.7-9.9)	630 (517-799)	0.48 (0.23-0.61)	26.03	3.09
	Beverton-Holt	15 (3.3-25)	630 (517-1,025)	0.48 (0.35-0.61)	25.98	3.03
Elochoman River	Random walk			1.36 (1.11-1.62)	51.04	12.38
	Constant recruitment		**626 (432-819)**	**0.86 (0.61-0.98)**	**38.66**	**0.00**
	Random walk with trend	1.8 (0.94-3)		1.24 (0.86-1.62)	51.44	12.78
	Hockey-stick	9.9 (1.8-10.5)	626 (432-1,109)	0.86 (0.61-0.86)	41.97	3.31
	Ricker	4.5 (2.7-6.9)	1013 (723-1,496)	0.73 (0.48-0.86)	39.51	0.85
	Beverton-Holt	25 (3.6-25)	626 (432-1,496)	0.86 (0.61-0.86)	41.88	3.22
Grays River	**Random walk**			**1.49 (1.24-1.62)**	**55.62**	**0.00**
	Constant recruitment		371 (141-716)	1.49 (1.24-1.74)	60.11	4.49
	Random walk with trend	1.3 (0.7-2.1)		1.36 (1.11-1.62)	57.87	2.26
	Hockey-stick	2.1 (1.08-9.6)	716 (371-1,176)	1.24 (0.98-1.36)	57.27	1.65
	Ricker	3 (1.2-7.2)	601 (371-1,865)	1.24 (0.86-1.36)	57.14	1.53
	Beverton-Holt	3.9 (1.3-12)	716 (371-3,359)	1.24 (0.98-1.36)	57.50	1.89
Kalama River	Random walk			1.36 (0.98-1.74)	51.46	12.57
	Constant recruitment		**7369 (4,917-9,821)**	**0.86 (0.48-0.98)**	**38.88**	**0.00**
	Random walk with trend	1.5 (0.85-3)		1.36 (0.86-1.62)	52.54	13.66

Table G.2.c cont.

	Hockey-stick	6 (1.8-9.3)	7,369 (4,917-9,821)	0.86 (0.48-0.98)	42.19	3.31
	Ricker	3.9 (2.4-9.3)	9,821 (7,369-14,724)	0.86 (0.61-0.98)	44.49	5.60
	Beverton-Holt	25 (6.9-25)	7,369 (4,917-11,047)	0.86 (0.61-0.98)	42.59	3.70
Mill Creek	Random walk			1.11 (0.86-1.36)	45.87	4.91
	Constant recruitment		**2,465 (1,389-3,542)**	**0.86 (0.48-1.11)**	**40.96**	**0.00**
	Random walk with trend	1.5 (0.92-2.4)		1.11 (0.73-1.24)	46.60	5.65
	Hockey-stick	5.1 (1.2-11)	2,465 (1,748-4,618)	0.86 (0.48-0.98)	44.27	3.31
	Ricker	3.3 (1.5-7.2)	3,183 (2,465-5,695)	0.86 (0.48-1.11)	44.61	3.65
	Beverton-Holt	12 (1.8-25)	2,824 (2,107-10,001)	0.86 (0.61-0.98)	44.12	3.16
Washougal River	Random walk			1.11 (0.73-1.36)	44.61	9.86
	Constant recruitment		**2,692 (2,000-3,383)**	**0.73 (0.35-0.86)**	**34.75**	**0.00**
	Random walk with trend	1.2 (0.7-1.8)		1.11 (0.73-1.36)	47.07	12.32
	Hockey-stick	8.4 (1.4-12)	2,692 (2,000-3,729)	0.73 (0.35-0.86)	38.06	3.31
	Ricker	8.1 (3.6-16)	4,075 (3,037-5,458)	0.73 (0.35-0.86)	37.34	2.59
	Beverton-Holt	25 (25-25)	2,692 (2,000-4,075)	0.73 (0.35-0.86)	38.68	3.93
Wind River[b]	Random walk			1.99 (1.24-2.5)	44.95	14.79
	Constant recruitment		208 (112-351)	1.11 (0.61-1.49)	36.52	6.36
	Random walk with trend	1.4 (0.6-3.9)		1.99 (1.24-2.5)	47.87	17.72
	Hockey-stick	20 (2.1-20)	255 (112-446)	1.11 (0.48-1.49)	40.07	9.91
	Ricker	**18 (9.9-25)**	**780 (494-1,018)**	**0.61 (0.23-0.86)**	**30.16**	**0.00**

Table G.2.c cont.

	Beverton-Holt	25 (25-25)	255 (112-494)	1.11 (0.48-1.49)	40.46	10.31
Clackamas River[c]	Random walk			0.86 (0.73-1.11)	68.84	22.66
	Constant recruitment		**447 (387-568)**	**0.61 (0.48-0.61)**	**46.18**	**0.00**
	Random walk with trend	1.02 (0.75-1.4)		0.86 (0.73-1.11)	71.19	25.01
	Hockey-stick	2.7 (1.5-3.9)	508 (387-568)	0.61 (0.35-0.61)	48.09	1.91
	Ricker	3.3 (2.1-5.1)	568 (508-750)	0.61 (0.35-0.61)	47.76	1.57
	Beverton-Holt	20 (4.2-25)	508 (447-629)	0.61 (0.48-0.61)	48.85	2.66

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference <2 are highlighted in light gray.

[b] Recruits based on natural-origin escapement, not preharvest.

[c] Recruits based on natural-origin escapement, not preharvest. Spawners based on total spawners, and the fraction of hatchery-origin is unknown.

Table G.2.d Lower Columbia River winter steelhead population parameter estimates and model comparison. Except as noted, recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.) Exceptions to these spawner and recruit definitions occur because of data limitations.

Population	**Model**[a]	**a**	**b**	**σ^2**	**AICc**	**Relative AICc**
East Fork Lewis River[b]	Random walk			0.98 (0.73-1.11)	14.83	3.19
	Constant recruitment		**86 (82-88)**	**0.23 (0.23-0.23)**	**11.64**	**0.00**
	Random walk with trend	0.6 (0.6-0.6)		0.48 (0.23-0.61)	21.15	9.51
	Hockey-stick	0.6 (0.6-1.08)	86 (82-90)	0.23 (0.23-0.23)	Infinity	Infinity
	Ricker	1.02 (0.65-1.4)	90 (84-95)	0.23 (0.23-0.23)	Infinity	Infinity
	Beverton-Holt	3.9 (1.02-25)	95 (84-132)	0.23 (0.23-0.23)	Infinity	Infinity
Clackamas River	Random walk			1.24 (1.11-1.36)	126.10	66.06
	Constant recruitment		**4,152 (3,696-5,063)**	**0.48 (0.35-0.61)**	**60.04**	**0.00**
	Random walk with trend	2.7 (2.4-3.3)		0.73 (0.61-0.73)	82.57	22.53
	Hockey-stick	7.5 (3.3-7.8)	4,152 (3,696-5,063)	0.48 (0.35-0.61)	62.41	2.36
	Ricker	6.6 (4.5-9.6)	5,063 (4,152-5,518)	0.48 (0.35-0.61)	66.14	6.10
	Beverton-Holt	25 (8.1-25)	5,063 (4,152-6,429)	0.48 (0.35-0.61)	62.93	2.89
Kalama River	Random walk			0.61 (0.48-0.86)	40.55	5.90
	Constant recruitment		**1,108 (952-1,419)**	**0.48 (0.35-0.61)**	**34.65**	**0.00**
	Random walk with trend	0.88 (0.7-1.15)		0.61 (0.48-0.73)	42.04	7.40
	Hockey-stick	2.4 (0.85-2.4)	1,108 (952-1,574)	0.48 (0.35-0.61)	37.50	2.85
	Ricker	2.1 (1.15-3.3)	1,263 (1,108-1,729)	0.48 (0.35-0.61)	36.70	2.05
	Beverton-Holt	5.1 (1.4-25)	1,419 (1,108-2,817)	0.48 (0.35-0.61)	36.79	2.15

Table G.2.d cont.

North Fork Toutle	Random walk			1.11 (0.35-1.74)	23.54	9.18
	Constant recruitment		**173 (131-214)**	**0.35 (0.23-0.48)**	**14.36**	**0.00**
	Random walk with trend	1.8 (1.1-3.3)		0.86 (0.23-1.24)	25.07	10.71
	Hockey-stick	9.6 (1.5-18)	173 (142-225)	0.35 (0.23-0.48)	21.36	7.00
	Ricker	4.5 (2.1-11)	235 (183-359)	0.61 (0.23-0.73)	26.47	12.11
	Beverton-Holt	25 (2.4-25)	183 (162-370)	0.35 (0.23-0.61)	21.63	7.27
South Fork Toutle	**Random walk**			**0.48 (0.23-0.73)**	**10.71**	**0.00**
	Constant recruitment		1,526 (1,224-1,828)	0.35 (0.23-0.35)	12.07	1.36
	Random walk with trend	0.94 (0.7-1.3)		0.48 (0.23-0.61)	17.31	6.59
	Hockey-stick	1.8 (0.7-20)	1,526 (1,299-1,903)	0.35 (0.23-0.35)	32.07	21.36
	Ricker	3.9 (0.83-9.9)	1,677 (1,526-3,186)	0.35 (0.23-0.35)	33.07	22.36
	Beverton-Holt	25 (1.15-25)	1,526 (1,375-3,186)	0.35 (0.23-0.35)	32.22	21.51
Sandy River	Random walk			0.23 (0.23-0.35)	4.92	8.98
	Constant recruitment		**2,696 (2,616-2,855)**	**0.23 (0.23-0.23)**	**-4.07**	**0.00**
	Random walk with trend	0.96 (0.83-1.08)		0.23 (0.23-0.35)	7.64	11.71
	Hockey-stick	1.3 (1.15-2.7)	2,775 (2,616-2,855)	0.23 (0.23-0.23)	0.01	4.08
	Ricker	2.7 (2.4-3.9)	2,775 (2,696-3,014)	0.23 (0.23-0.23)	0.07	4.14
	Beverton-Holt	25 (7.8-25)	2,855 (2,696-3,173)	0.23 (0.23-0.23)	0.27	4.33

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference <2 are highlighted in light gray.

[b] Recruits based on natural-origin escapement, not preharvest.

Table G.2.e Lower Columbia River summer steelhead population parameter estimates and model comparison. Recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.)

Population	Model[a]	a	b	σ^2	AICc	Relative AICc
Kalama River	Random walk			1.49 (1.24-1.87)	76.34	26.72
	Constant recruitment		**906 (687-1,343)**	**0.73 (0.61-0.86)**	**49.63**	**0.00**
	Random walk with trend	0.6 (0.6-0.6)		1.24 (0.86-1.49)	68.72	19.09
	Hockey-stick	0.8 (0.6-2.7)	906 (687-1,343)	0.73 (0.48-0.86)	52.42	2.79
	Ricker	0.65 (0.6-1.3)	1,343 (906-1,781)	0.86 (0.61-0.98)	55.69	6.06
	Beverton-Holt	5.1 (0.83-25)	1,125 (906-1,562)	0.73 (0.48-0.86)	52.48	2.85
Washougal River	Random walk			0.61 (0.48-0.61)	20.84	7.45
	Constant recruitment		**178 (151-218)**	**0.35 (0.23-0.48)**	**13.39**	**0.00**
	Random walk with trend	0.8 (0.6-1.04)		0.48 (0.23-0.61)	21.87	8.48
	Hockey-stick	1.8 (0.7-8.7)	178 (151-272)	0.35 (0.23-0.48)	17.32	3.93
	Ricker	1.8 (0.92-3)	205 (178-299)	0.35 (0.23-0.48)	19.62	6.23
	Beverton-Holt	7.2 (1.1-25)	205 (164-489)	0.35 (0.23-0.35)	17.16	3.77
Wind River	Random walk			0.48 (0.35-0.61)	13.88	11.19
	Constant recruitment		486 (419-587)	0.35 (0.23-0.35)	11.50	8.81
	Random walk with trend	**0.65 (0.6-0.7)**		**0.23 (0.23-0.23)**	**2.69**	**0.00**
	Hockey-stick	0.65 (0.6-0.75)	855 (486-855)	0.23 (0.23-0.23)	7.82	5.12
	Ricker	0.75 (0.65-0.9)	1,290 (1,089-1,290)	0.23 (0.23-0.23)	8.20	5.50
	Beverton-Holt	1.02 (0.85-1.3)	1,290 (1,290-1,290)	0.23 (0.23-0.23)	9.63	6.93

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference < 2 are highlighted in light gray.

Table G.2.f Columbia River chum salmon population parameter estimates and model comparison. Recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.)

Population	**Model**[a]	**a**	**b**	**σ^2**	**AICc**	**Relative AICc**
Grays River	Random walk			1.11 (0.86-1.49)	84.72	14.88
	Constant recruitment		402 (319-569)	0.86 (0.61-0.98)	69.85	0.00
	Random walk with trend	1.3 (0.94-1.8)		1.11 (0.73-1.36)	85.37	15.52
	Hockey-stick	25 (1.15-25)	402 (319-1,069)	0.86 (0.61-0.98)	72.44	2.59
	Ricker	2.1 (1.4-4.2)	819 (569-1,152)	0.98 (0.73-1.24)	82.29	12.45
	Beverton-Holt	25 (1.8-25)	485 (402-1,152)	0.86 (0.61-0.98)	72.38	2.53
Hardy Creek	Random walk			1.49 (1.11-1.99)	145.19	51.33
	Constant recruitment		180 (149-212)	0.73 (0.61-0.98)	93.86	0.00
	Random walk with trend	1.4 (0.96-2.1)		1.49 (1.11-1.87)	145.21	51.35
	Hockey-stick	25 (7.8-25)	180 (149-244)	0.86 (0.61-0.98)	103.63	9.77
	Ricker	4.5 (2.4-7.8)	338 (244-433)	1.11 (0.86-1.49)	127.56	33.70
	Beverton-Holt	25 (9-25)	212 (149-244)	0.86 (0.61-0.98)	103.57	9.71
Lower Gorge	Random walk			2.12 (1.36-2.5)	227.65	100.53
	Constant recruitment		474 (383-565)	0.73 (0.61-0.98)	127.12	0.00
	Random walk with trend	1.5 (0.96-2.4)		2.12 (1.36-2.5)	227.97	100.85
	Hockey-stick	25 (25-25)	383 (383-474)	1.24 (0.73-1.49)	172.21	45.10
	Ricker	6.3 (3.3-16)	929 (656-1,658)	1.62 (0.98-1.99)	200.54	73.42
	Beverton-Holt	25 (25-25)	474 (383-565)	1.24 (0.73-1.49)	173.15	46.03

[a] The a, b, and σ2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference < 2 are highlighted in light gray.

Table G.2.g Upper Willamette River spring chinook salmon population parameter estimates and model comparison. Except as noted, recruits are based on estimates of preharvest natural-origin fish, and spawners are based on the estimate of natural-origin spawners plus half of the hatchery-origin spawners (hatchery-origin spawners are assumed to have lower reproductive success than natural-origin spawners.) Exceptions to these spawner and recruit definitions occur because of data limitations.

Population	Model[a]	a	b	σ^2	AICc	Relative AICc
Clackamas River[c]	Random walk			0.73 (0.61-0.86)	92.86	11.27
	Constant recruitment		1,238 (1,036-1,440)	0.86 (0.73-0.98)	102.00	20.41
	Random walk with trend	1.2 (0.99-1.5)		0.73 (0.61-0.86)	92.90	11.31
	Hockey-stick	1.5 (1.2-2.1)	2,250 (1,845-2,655)	0.61 (0.48-0.73)	82.03	0.43
	Ricker	2.1 (1.5-2.7)	2,048 (1,845-2,858)	0.61 (0.48-0.73)	81.59	0.00
	Beverton-Holt	2.1 (1.5-3.3)	3,465 (2,453-5,287)	0.61 (0.48-0.73)	82.67	1.08
McKenzie River[c]	Random walk			0.86 (0.61-0.98)	65.10	24.05
	Constant recruitment		2,242 (1,984-2,760)	0.48 (0.35-0.61)	41.05	0.00
	Random walk with trend	0.94 (0.75-1.3)		0.86 (0.61-0.98)	67.34	26.28
	Hockey-stick	3 (1.3-9.6)	2,242 (1,984-2,760)	0.48 (0.35-0.61)	43.62	2.57
	Ricker	2.7 (1.8-4.5)	2,760 (2,242-3,278)	0.61 (0.35-0.61)	50.62	9.56
	Beverton-Holt	25 (5.1-25)	2,242 (1,984-3,019)	0.48 (0.35-0.61)	44.62	3.57

[a] The *a*, *b*, and σ^2 parameters for each model are described in Table G.1. The 95% confidence intervals on the parameter estimated are shown in parentheses. The AICc best approximating model for each population is highlighted in dark gray, and any models with an AICc difference <2 are highlighted in light gray.

[c] Recruits based on natural-origin escapement, not preharvest. Spawners based on total spawners, and the fraction of hatchery-origin is unknown.

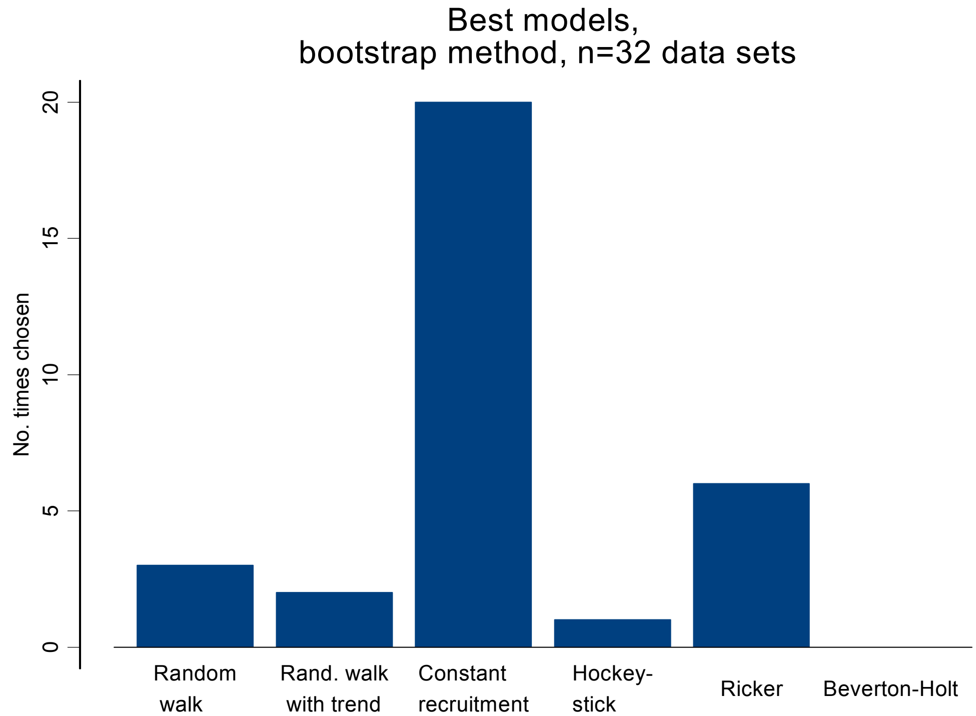

Figure G.9 Frequency of recruitment models selected as the best approximate models for 32 Willamette and Lower Columbia salmon populations. Models were selected using relative AICc method (see Table G.2).

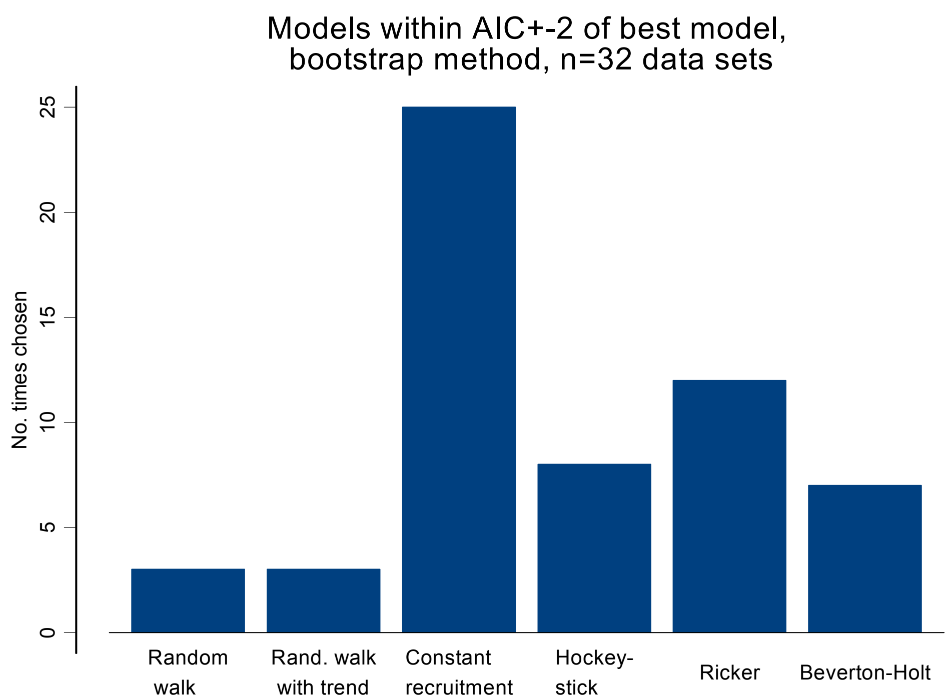

Figure G.10 Frequency of recruitment models selected as the best or near-best approximate models for 32 Willamette and Lower Columbia salmon populations. Models selected using relative AICc methods. Models considered near best had AIC difference values less than 2 (see Table G.2).

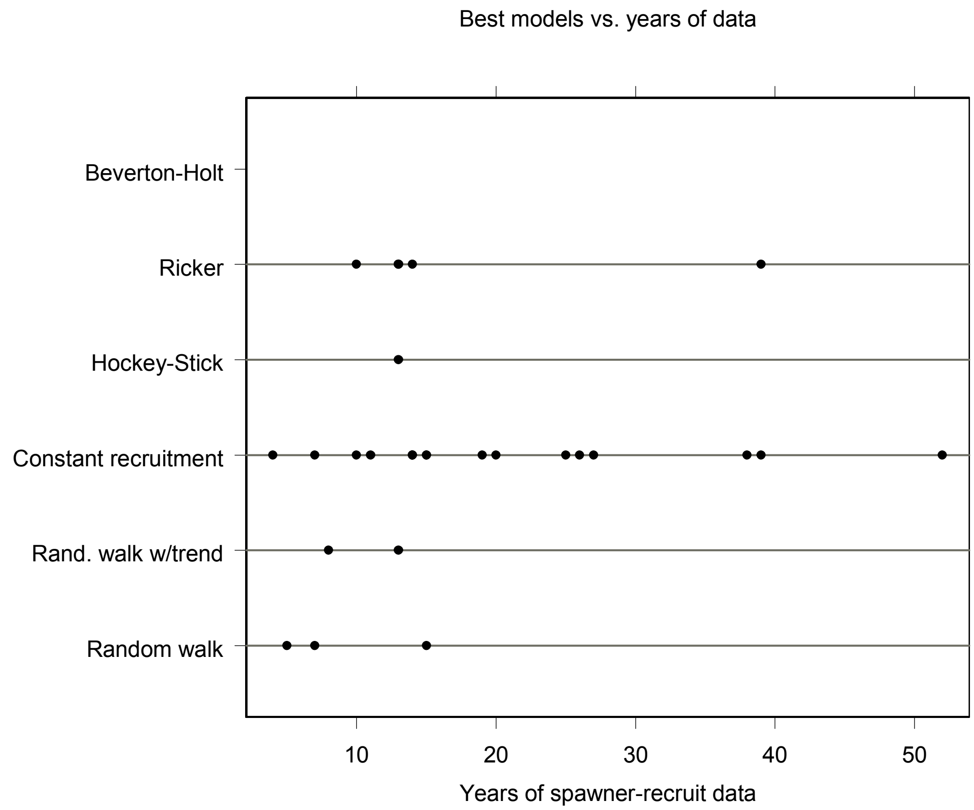

Figure G.11 Best model as a function of the number of years of spawner-recruit data (see Table G.2).

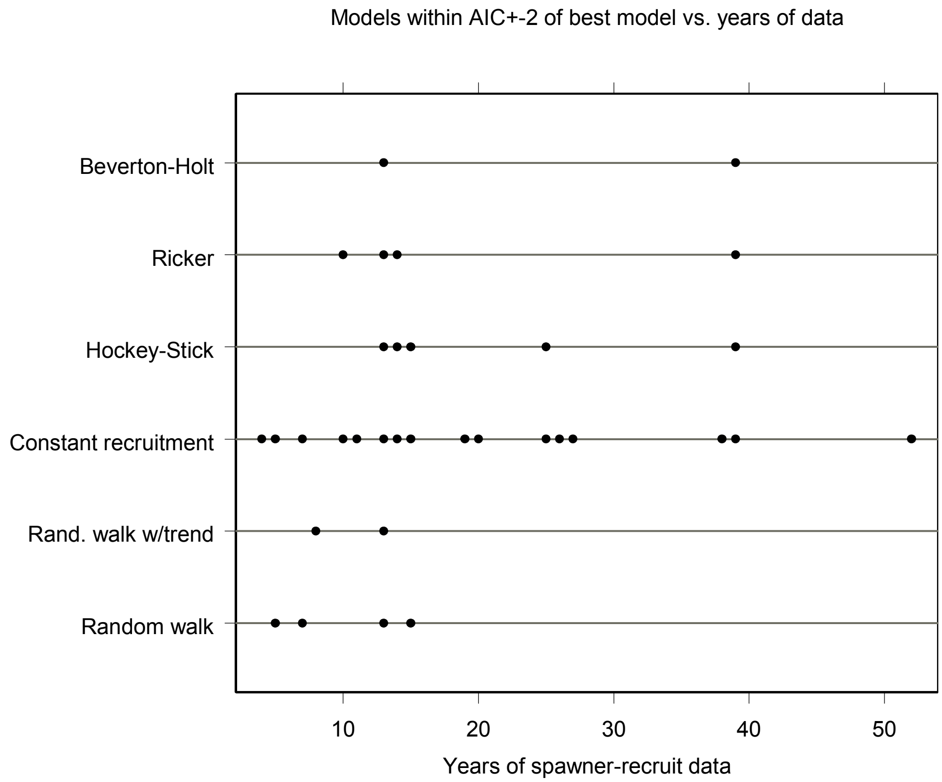

Figure G.12 Best model and near-best models as a function of the number of years of spawner-recruit data (see Table G.2). Models considered near best had AIC difference values less than 2.

Model Section Using Simulated Data

Although the observed data do not provide much information about the exact value of intrinsic productivity in a population, the selection of the constant recruitment model does suggest on the surface that productivity is greater than 1 and that the population is simply showing random fluctuations around a carrying capacity. However, this conclusion may be overly optimistic. We simulated a number of population trajectories using a hockey-stick model with an intrinsic productivity of 1. The populations were started substantially below the ceiling, so the trajectories were basically a random walk with an upper bound. We then calculated the recruits-per-spawner values from the trajectories, calculated parameters for the six models, and applied the AIC model selection approach (Figures G.11). In most of these examples, the best approximating model was either the constant recruitment model or the random-walk model. We speculate that the constant recruitment model is commonly selected as the best model because a short time series that samples a random-walk process appears as a cloud of points on a spawner-recruit graph. In the absence of data at very low (or very high) spawner numbers, the data are likely to fit a constant recruitment model. This is particularly true if the there is any sort of population ceiling that leads to a flattening of the spawner-recruit cloud.

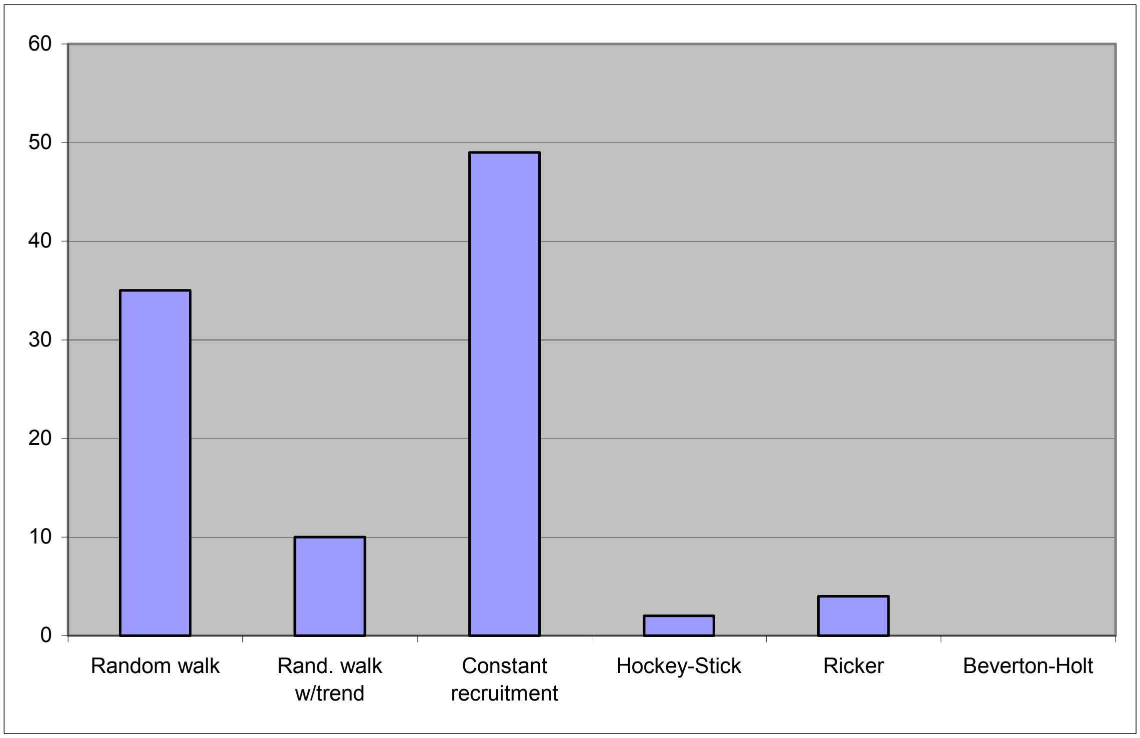

Figure G.11 Frequency of models selected as the best approximating model for simulated population trajectories. We simulated 100 25-year population trajectories with a hockey-stick model with an initial population size of 5,000, carrying capacity of 50,000, intrinsic productivity of 1, with log-normal process error (normal distribution mean = 0 and variance = 0.6). The variance of 0.6 is similar to that observed for Willamette/Lower Columbia populations (see Table G.2). The viability curves were generated for a semelparous population where the average percentages of individuals spawning at a given age are: age 1 = 0%, age 2 = 1%, age 3 = 19%, age 4 = 57%, and age 5 = 23%. This life-history structure is typical to that observed for chinook salmon.

Conclusions

Analysis of both the WLC populations and simulated trajectories suggest that the adult recruits-per-spawner data typically available for salmon populations will be inadequate to estimate intrinsic productivity. The lack of data at small spawner abundances make recruit curve–based productivity estimates highly uncertain.

Recruitment models are a foundation of harvest modeling and have been proposed as metrics for viability criteria. Before applying these models, it is important to have a solid understanding of the uncertainties involved in parameter estimation and model selection.

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